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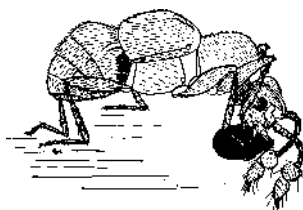
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The Tree-Hole Habitat with Emphasis on the
Pselaphid Beetle Fauna

Orlando Park, Stanley Auerbach, and Glenna Corley

Northwestern University

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A preliminary study of the Pselaphidae (Coleoptera) of Mexico, 1943, Chicago Acad. Sci., Bull., vol. 7, no. 3, p. 171-226, pl. 1-3.	.60
New and little known Pselaphidae (Coleoptera) from Brazil, Colombia, and Mexico, with keys to Mexican genera and species, 1944, <i>Ibid.</i> , no. 4, p. 227-267, pl. 1-2.	.50
A preliminary study of the Pselaphidae (Coleoptera) of the Guianas, 1945, <i>Ibid.</i> , no. 6, p. 277-327, pl. 1-7.	.60
Further studies in Pselaphidae (Coleoptera) of Mexico and Guatemala, 1945, <i>ibid.</i> , no. 7, p. 331-443, pl. 1-11.	\$125
A new pselaphid beetle from Brazil associated with termites, 1946, <i>Ibid.</i> , no. 8, p. 445-451, pl.	.10
Checklist of Pselaphidae (Coleoptera) known from Guatemala, 1946, <i>Ibid.</i> , no. 9, p. 457-468.	.25
Revision of the fifty-fourth group of the pselaphid genus <i>Reichenbachia</i> (Coleoptera), 1946, <i>Ibid.</i> , no. 13, p. 499-511, pl. 1-2.	.35
Observations on <i>Batrisodes</i> (Coleoptera: Pselaphidae), with particular reference to the American species east of the Rocky Mountains, <i>Ibid.</i> , vol. 8, 1947, no. 3, p. 45-132, pl. 1-11.	\$160
Checklist of the genus <i>Batrisodes</i> (Coleoptera: Pselaphidae), <i>Ibid.</i> , no. 4, 1948, p. 137-169.	.75
New and little known <i>Reichenbachia</i> (Coleoptera: Pselaphidae) from Guerrero, and their zoogeographic integration. <i>Ibid.</i> , no. 6, 1948, p. 181-192, 1 pl.	.50
Studies in Japanese Pselaphidae (Coleoptera), I. Introductory materials, checklist, and key to genera. <i>Ibid.</i> , no. 8, 1948, p. 203-221.	.50
The genus <i>Connodontus</i> (Coleoptera: Pselaphidae). <i>Ibid.</i> , no. 11, 1949, p. 251-266, pl. 1, 2.	.50
Pselaphid beetles of an Illinois prairie: The fauna, and its relation to the prairie peninsula hypothesis, by Orlando Park, Stanley Auerbach, and Marie Wilson. <i>Ibid.</i> , no. 12, 1949, p. 267-276, pl. 1, 2.	.50
New species of nearctic pselaphid beetles and a revision of the genus <i>Cedius</i> . <i>Ibid.</i> , no. 16, 1949, p. 315-343, pl. 1-8.	.70
The second record of predation on pselaphid beetles, by Orlando Park and R. A. Edgren. Nat. Hist. Misc. no. 54, 1950, p. 1-2.	.15

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The Bulletin of the Chicago Academy of Sciences was initiated in 1883 and volumes 1 to 4 were published prior to June, 1913. During the following twenty-year period it was not issued. Volumes 1, 2 and 4 contain technical or semi-technical papers on various subjects in the natural sciences. Volume 3 contains museum reports, descriptions of museum exhibits, and announcements.

Publication of the *Bulletin* was resumed in 1934 with volume 5. It is now regarded as an outlet for short to moderate-sized original papers on natural history, in its broad sense, by members of the museum staff, members of the Academy, and for papers by other authors which are based in considerable part upon the collections of the Academy. It is edited by the Director of the Academy with the assistance of a committee from the Board of Scientific Governors. The separate numbers are issued at irregular intervals and distributed to libraries, scientific organizations, and specialists with whom the Academy maintains exchanges. A reserve is set aside for future need as exchanges and the remainder of the edition offered for sale at a nominal price. When a sufficient number of pages have been printed to form a volume of convenient size, a title page, table of contents, and index are supplied to libraries and institutions which receive the entire series.

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CONTENTS

Introduction	19
General Ecology of Tree Holes	20
The Pselaphid Beetle Fauna	35
Summary	40
Literature Cited	42

INTRODUCTION

During the past few decades there has been an increasing interest on the part of biologists in the general subject of tree holes. This awareness has been accelerated primarily as the result of the stimulus from two economic aspects. For example, the tree hole as a source of spread of wood rot fungi through living trees has interested forestry in general and economic mycologists in particular. Furthermore, the tree hole as a breed-

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ing ground for certain mosquitoes has interested scientists in several phases of economic entomology. By the late 1920's the tree hole was recognized as a special habitat niche in the forest community, but little attention was given to its general organization and development.

In the course of studying the pselaphid beetles of the Chicago Area, it was found that quite a few species were relatively more abundant in tree-hole mold than in the ecologically related log mold of the forest floor, and in one instance a new species of pselaphid is known from tree holes only (Park, 1949) .

Consequently, previous notebook entries were reexamined, and a series of tree hole samples was collected to accumulate more information concerning this habitat. In all, 36 tree holes were examined. The data included species of tree, community, shape of tree-hole orifice, height of hole above the ground, size of cavity, direction in which the hole faced, degree of disturbance as a consequence of man's activities, locality, date, time sample was collected, and temperature of the tree-hole mold. Each sample was returned to the laboratory as soon as feasible, the tree-hole mold was weighed (wet weight in grams) , and the sample placed in a Berlese funnel for extraction of arthropods. The samples were berlesed until very dry (from four to fifteen days, depending upon sample size and amount of contained moisture) , the mold was then reweighed (dry weight in grams) , and the percentage of the free water content calculated. The arthropods were collected in 95 per cent ethyl alcohol and examined for pselaphid beetles. Finally, several samples were counted to arrive at a quantitative picture of tree-hole inhabitants. In addition to this direct analysis of tree holes, a series of tree frogs (*Hyla v. versicolor*) was borrowed in the expectation that an analysis of their stomach contents might throw additional light on a possible tree-hole food web. A report of progress has been published previously (Park, Auerbach and Corley, 1949).

GENERAL ECOLOGY OF TREE HOLES

A tree hole may be defined as any tree cavity, produced through the action of extrinsic factors, that is in direct contact with the external environment at some point in its development. In this broad definition are included subterranean tree holes (root holes) , concerning which almost nothing is known, and epigeal tree holes, or tree holes in the conventional sense. It is with these latter that we are concerned here.

Such tree holes vary greatly in size. They may be minute cylindrical pits just reaching sapwood, or large, irregularly shaped cavities that involve a great deal of heartwood, or any intermediate stage between such extremes. A large heartwood cavity may open to the exterior by

several orifices. The orifice may be almost any shape, but usually is roughly circular, or fusiform, or triangular. The orifice may open on any face of the tree. Tree holes may occur at any height, from those at ground level (basal tree holes), upwards. Generally, basal tree holes are the most obvious. Several tree holes are illustrated (Pl. I, II) to show this range in variation. Such microhabitats are to be expected wherever trees grow, from equatorial rain forests northward to the taiga, and from sea level to the timber line.

Usually tree holes have their origin in living trees, and one of the differences between the tree-hole habitat and the decaying log on the forest floor is that the later is dead whereas the former is more or less surrounded by living tree tissues. Basal tree holes may eventually, or from the start, have their floor formed by the soil of the forest, but in general the tree-hole mold is formed within a living tree.

Although diverse in so many aspects, tree holes are formed apparently by an initial fracture of the bark that exposes the sapwood. This is followed by weathering of this fracture and the attack on the exposed wood by fungi, and probably bacteria. Usually this fracture deepens with time. The initial fracture may arise by many environmental actions. These may be separated at once into physical and biotic agencies. Among the former are included fire, storm winds, ice splits, lightning splits, limbs torn away by lightning, and the functional tree hole may be continually altered by rain, snow, further ice fractures and indirect erosion by wind.

Of the physical influences, fire is especially important. The secondary infection by parasitic fungi following fire wounds may be at any point on the tree (e.g., branch stubs) but butt wounds by fire are most common (Hepting, 1941; Hepting and Chapman, 1938) .

In a study of Appalachian oaks, yellow poplar, and basswood, Hepting and Hedgcock (1937) found that, of trees examined, 47.1 per cent had wounds that were caused apparently by fire, 0.6 per cent had lightning wounds, and 1.5 per cent had wounds from other causes. Butt wounds were important, since 77 per cent of the total cull volume was the result of basal or butt defects, 20 per cent was due to top rot and 3 per cent from miscellaneous causes. Of trees that had no basal wounds, only 6 per cent had butt rot.

Such numerous wounds allow many injurious fungi to infect the wood, including *Stereum*, *Hydnum*, *Armillaria*, *Fistulina*, *Poria*, *Polyporus*, and *Fomes*. *Stereum gausapatum* is an especially important species. This fungus is almost coextensive with the hardwood forests of North America, and although most common on oaks, is reported from maples, beech, chestnut, hornbeam, poplars and ash, among other trees (Herrick, 1939) ; in 1718 oak infections, this fungus caused 707 (Davidson and Vaughn, 1942) ; in butt rot in sprout oak stands the average annual

penetration rate of *gausapatum* ranged from 2 to 3 inches, with a maximum rate of 15 inches, and decay caused by this species was found as high as 200 inches (Roth and Sleeth, 1939).

These observations explain why the authors found basal tree holes to be more common than the higher orifices among the trees examined, and the bearing of this on the tree-hole fauna will be discussed later.

Depending upon kind of tree, a demonstrable wound gum may be produced just beneath the scarred trunk surface and this gum often protects the tree from fungus infection (Hepting, 1935). Healing of the wound by the tree is a more gradual protective function. In oaks (Hepting and Hedgecock, 1937) , the callus folds converge at an average annual rate of from 0.45 inch to 0.31 inch, in basal wounds.

Nevertheless, tree wounds are exploited by biotic agents rapidly enough to cause considerable damage, and many animals attack tree trunks and branches, whether wounded or not.

Such agents are numerous. These are chiefly insects (Graham, 1939), and include wood-borers that tunnel living tree tissues (larvae of buprestid and cerambycid beetles and larvae of many siricid hymenopterans, to name a few). Other insects attack wood that has been softened by fungi, for example, the carpenter ants (*Camponotus*) may attack decayed heartwood in a living tree, and the pigeon horn-tail (*Tremex columba*) is one of the few siricids that is said to attack decayed wood., In the tropics, termites commonly attack living trees, and these insects and ants are reported to invade decayed wood behind fire scars in the Delta area of the lower Mississippi River (Hepting, 1935).

Most woodpeckers attack living trees for food and in excavating a nest, although certain species may chisel out a cavity in a dead tree, or they may exploit a tree hole formed by another agency. Rabbits and deer may be included in the general category of biotic agents that attack trees, but man is a greater menace through careless wounding of trees, injuries caused in logging, and indirectly by starting forest fires.

Of course, many tree wounds may not be invaded by fungi, but where the tree hole is initiated, a further set of complex reactions takes place, along one of several lines that converge once more when the tree dies. This entire process, involving one of several parallel tree-hole microsere, is suggested by a very diagrammatic figure (Fig. 1) , and may be termed the tree-hole complex. Involved are numerous parallel, converging, or diverging events that may be competitive or cooperative with one another. Eventually, when the tree falls to the ground, the tree-hole microsere passes into the decaying-log microsere, and in turn

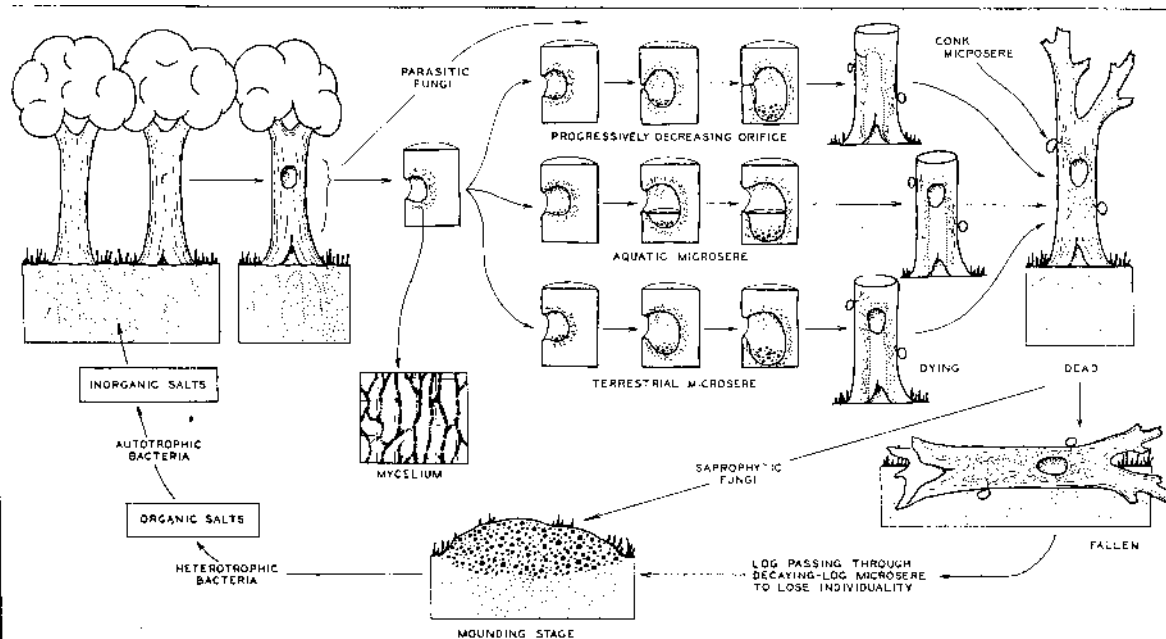


DIAGRAM OF ALTERNATIVE COURSES OF TREE HOLE DEVELOPMENT, AND INTEGRATION WITH THE DECAYING-LOG MICROSERE IN THE METABOLIC CYCLE OF THE COMMUNITY.

Figure 1. Diagram of tree-hole complex. For discussion see text.

the log loses its individuality to become incorporated once more in the general cycle of community energetics.

Within this complex, one of the most important influences in the development of tree holes is mycological. In respect to this particular habitat type, we are not directly concerned with the entrance of parasitic fungi through leaf stomata, or the penetration of young trees by such fungi before cork is formed in the bark. Rather, the colonization of more mature trees by parasitic fungi that gain entrance through a fracture of the protective bark covering is a logical step in formation of certain kinds of tree holes. Such a development is a second stage, after the action of one or more of the primary agents has exposed the wood. These parasitic fungi are numerous, vary in host specificity, are differentially affected by climatic and edaphic factors, and may develop rapidly or require several decades to produce demonstrable results. This field of endeavor includes numerous academic and practical problems in ecology, general botany, mycology, agriculture, forestry, and conservation (Baxter, 1943; Boyce, 1938; Hawley and Stickel, 1948; Hepting and Kimmey, 1949).

In general, exploitation of the bark fracture may be consummated by (1) sapwood rots, attacking both young and old trees; (2) heartwood rots, attacking trees after heartwood has formed; (3) subterranean root rots attack both young and old trees and may spread from root to root to infect neighboring trees and possibly form root holes; (4) cankers of stem and branch that may be general (e.g., *Nectria* that attacks many hardwoods) or more specific (e.g., *Strumella*, parasitizing oaks).

With favorable climatic and edaphic conditions, the fracture deepens through time and the developing tree hole is occupied by animals that can tolerate the relatively dark, moist niche in the living tree. At this point the tree-hole microsera may deviate in one of several ways (Fig. 1).

The first of these is uncommon; namely, the tree grows at the lip of the fracture so that the orifice of the tree hole becomes progressively smaller. The observations of J. D. Brown (Elton, 1927) provide an example of this variation in the cycle. He observed occupants of a tree hole over a period of years. Initially the hollow in a beech tree was occupied by a nesting owl. As the orifice grew smaller, this tree-hole cavity was used by nesting starlings. Still later, the opening was too small for birds and was used by wasps. Eventually, the growth of the tree closed the orifice completely.

Where tree holes can receive and retain water, either for a season or much longer, an aquatic microsera develops. Such tree-hole reservoirs, then, parallel temporary or permanent ponds, as the case may be, and may fill up by deposition of tree-hole mold from the walls of the cavity (Allee, Emerson, Park, Park, and Schmidt, 1949).

Such aquatic reservoirs often have restricted or endemic species, as evidenced by the relatively better known mosquito fauna of tree holes (cf. Dalziel, 1920; Headlee, 1921; Keilin, 1927, 1932; Jenkins and Carpenter, 1946; Woke, 1947; Chow, 1949; Causey and Dos Santos, 1949; Elton, 1949; Bates, 1949a) . The data accumulated refer chiefly to the larvae of tree-hole mosquitoes, their parasites and their ecology. The "tree-hole mosquito, " *Anopheles barberi*, breeds exclusively in the water of tree holes, and the adults seldom are found far from this habitat (Headlee, 1921) . In an admirable survey of tree-hole mosquitoes of nearctic North America, Jenkins and Carpenter (*loc. cit.*) found that their distributions were limited northward chiefly by long winters, with associated relatively low temperatures, and limited in the midwest chiefly by the grassland biome. These authors list eight species and one subspecies, divided among four genera, confined to tree holes for breeding, or nearly so. These are *Anopheles barberi*, four species of *Aedes* (*alleni*, *thibaulti*, *triseriatus*, *varipalpus*) , two species of *Orthopodomyia* (*signifera*, *alba*) , *Megarhinus r. rutilus* and *M. r. septentrionalis*. Two of these, under laboratory conditions, are known to carry certain diseases of interest to man: *Anopheles barberi* (malaria) and *Aedes triseriatus* (yellow fever). Even with tree-hole mosquitoes, a great deal remains to be done, especially accumulation of quantitative data in an attempt to clarify environmental relationships of larvae, and the closer attention to limiting factors in their ecological distribution (Bates, 1949a) .

In tropical America, Bates reports a great variety of sabethine mosquitoes that inhabit tree holes, as well as the tropicopolitan genus *Megarhinus*.

In general the natural foods of most mosquito larvae are the bacteria, yeasts and protozoans that they strain from the water with their oral brushes, and in the tree holes these micro-organisms would be the tree-hole plankton. Interestingly enough, there are other tree-hole mosquitoes whose larvae are predaceous, such as *Megarhinus*, certain sabethine genera, and a few anophelines. The latter are not predaceous as a rule, but the tree-hole breeding *Anopheles barberi* (Howard, Dyar, and Knab, 1913), *Anopheles culiciformis* (Christophers and Chand, 1916) and *Anopheles barianensis* (Christophers, 1933) are said to be predaceous. The last mentioned is said to attack crushed insects that are thrown on the surface of the water. Thus the tree holes under discussion have a plankton that is fed upon by certain mosquito larvae, and these in turn are eaten by predaceous mosquito larvae.

Where the tree-hole water is lost and replenished periodically, many of the plankters probably encyst during the "dry" period. In certain tree holes in tropical rain forest, the tree-hole mosquitoes maintain the species by a diapause in the egg stage during the dry periods (Bates, 1949b) .

In the tropics the tree-hole reservoirs include tadpoles in the food web. Dunn (1931) discusses this association in Panama, where the tadpoles of the terrestrial dendrobatid frog (*Dendrobates auratus*) are transported into the water by the adult male. Again, the egg masses of another tree frog, *Agalychnis dacnicolor*, are suspended on the tree trunk, above the water.

Turning to the terrestrial microsere, with which we are concerned more particularly at this time, it should be noted that the tree-hole fauna essentially is an extension of the floor fauna, especially the arthropod fauna of log mold. This general ecological similarity increases as the tree-hole cavity deepens, the tree dies and this habitat merges into the decaying-log microsere (Fig. 1). The tree hole's fauna is dependent, in part, both qualitatively and quantitatively, on such physical factors as the moisture content and temperature of the mold, as well as size of cavity and distance from the ground.

In general, moist, warm tree-hole mold has a higher population density than dry, cool mold. Furthermore, the arthropod fauna tends to increase in numbers of species and individuals with increase in amount of mold. Other things being favorable, there is a faunal increase with increase in the size of the cavity and the lower the tree-hole orifice, the larger and more diversified the arthropod fauna. We have noted the nesting of vertebrates in tree holes, or hollow trees with tree-hole orifices. Such residents include owls, woodpeckers, deer mice and flying squirrels (Anthony, 1937; Clements and Shelford, 1939; Pearse, 1939; Pearson, 1936; Trippensee, 1948). Often such cavities are used by a succession of occupants. For example, woodpeckers may be followed by flying squirrels, and hairy and downy woodpeckers may be followed by the screech owl or black-capped chickadee (Shelford, 1913) .

Sviridenko (1945) found that the number of forest mice and mouse-like rodents increased with the increase of forest tree holes. In many instances, the tree-hole habitat is a factor in maintenance of population level of even relatively large mammals. For example, Brown and Yeager (1943) found that, among the possible den sites, tree cavities ranked highest with the raccoon, and that such niches were important in maintaining the numbers of this species.

Where such birds and mammals occupy a tree cavity, their ectoparasites (on occasion lice, mallophagans, fleas, mites and lepidopteran beetles) augment the local population; their faeces form a source of food for other organisms; their food stores (e.g., the substantial stores of nuts by flying squirrels) are shared by still other organisms; all of these secondary residents are preyed upon by predaceous and parasitic insects; the several food supplies are sources of nourishment for bacteria and fungi. Such

assemblages form ancillary appendages to the biota of the tree tissues (parasitic fungi, buprestid and cerambycid beetle larvae if the tree is living, or saprophytic fungi, elaterid and tenebrionid beetle larvae if the tree is dead), and the biota of the tree-hole mold that slowly accumulates in the expanding cavity.

Tree holes may be occupied by comb-making bees, carpenter ants, and, in parts of their ranges, the ants *Aphaenogaster fulva* and *tennesseensis*. Where ants are entrenched, the normal arthropod fauna of the tree-hole mold may be greatly decreased.

Insects are numerous in tree holes (Snow, 1944), and, as discussed later, may include a relatively high density of certain species found sparingly in the related log-mold habitat. Crane fly and mosquito adults are found resting on the walls of the cavity. In the tree-hole mold are myriads of collembolans, and various genera of beetles and ants. These smaller insects belong to various trophic levels and include herbivores, predators, scavengers, and parasites. Among beetles, Carabidae, Staphylinidae, Pselaphidae and Ptilidae are especially abundant.

Apparently centipedes and millipedes are not common, but the arachnid fauna is impressive, considering the relatively small volume of the habitat. Spiders and pseudoscorpions are to be found in the tree-hole mold, and spiders and phalangids cling to the cavity walls. The acarinids are numerous, and include parasitid, tyroglyphid, trombid, hoplodermatid and oribatid mites. The Oribatidae rival the collembolans in numbers. Not only is the family important as an herbivorous assemblage, but certain of these mites are suspected of vectoring fungus infections, such as Dutch elm disease (Jacot, 1934) . Apparently they can inhabit even the high tree holes, and have been observed climbing trees (Jacot, 1930).

Most of these insects and arachnids are small and form a cryptozoic fauna, in the sense of Cole (1946), and are a part of the edaphon, in the sense of France (1914).

Tree frogs should be found in tree holes on occasion, but no specific record of this is known to the authors. Nevertheless, a series of *Hyla v. versicolor* was borrowed for the purpose of analyzing their stomach contents. This was more desirable when it was learned also that very little information was available on the food of this amphibian. These data are presented in Table I.

In this table the contents of twenty-six stomachs are tabulated. This obviously small sample is suggestive. Almost half of the stomachs were empty, except for the frequent presence of nematode worms. This lack of food items may have been a result of the specimens not being killed soon enough after their capture. Of the fourteen specimens that had food in their stomachs, the order of abundance was: (1) ants, (2) stem fiber and seeds, (3) pieces of log mold, phalangids, heteropterans, (4) oribatid

Table I. Stomach Contents of *Hyla v. versicolor*

Kinds of Items	1	23	4	5	6	78	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	items
Fine sand grains (0.2-1.5 mm. diam.)							a+												a	a					3
Pieces of log mold						1		a	1		a														4
Strips of stem fiber					2	2	3			4	4										1				6
Compositaceae flower head, with pappi								1																	1
Seeds											4	2				a	3								6
Phalangida													1			2	f	2							4
Oribatidae							1	3			4														3
Spider																f									1
Entomobryidae											1														1
Sminthuridae																									1
Heteroptera											f		f			f									4
Cercopidae (<i>Lepyronia</i> ?																1									1
Pieces_ of chitin																									1
Insect legs						f			f		f														3
Beetle larva						f																			1
Scarabaeidae																									1
Weevil (<i>Conotrachelus</i> ?)																									1
Moth (Noctuidae)																		3							1
Caterpillar																									1
Dipterous larva																					f				
Dipterous adult																									1
Crane-fly adult												f													1
Ant (Misc.)							1									4				1					3
<i>Lasius n. americanus</i> ?													2		7	2	1								4
<i>Aphaenogaster</i>					5					1		1													3
Total items per stomach	0	00	0	0	4	60	5	4	1	3	6	3	3	0	5	4	7	0	1	5	0	0	0	0	
Percentage of items in a stomach with respect to total of kinds o food items (e.g., 25)	0	00	0	0	16	240	20	16	4	12	24	12	12	0	20	16	28	0	4	20	0	0	0	0	

food items (e.g., 25)

*No. 1-5, Dune Acres, Porter Co., Indiana, (Chicago Academy of Sciences, No. 1861-4, 5804)

No. 6-14, Hopkins Park, Kankakee Co., Illinois, (Chicago Academy of Sciences, No. 4724-32)

No. 15-25, near Burlington, Racine Co., Wisconsin, (Richard Edgren, No. 510, 529, 542, 552-3, 557, 628, 670.1, 686-8) +

a, abundant; f, fragments.

mites, unidentifiable pieces of insect legs, and (5) a miscellany of other arachnids and insects. Twelve of these fourteen frogs had eaten plant products. This may suggest a much more omnivorous diet for tree frogs than would be imagined, or it may indicate that tree frogs are careless or ineffective feeders and so pick up a great deal of accidental material, or the sample may be so small that the preponderance of vegetable products is not an accurate picture of the species' feeding habits. Certainly, the specimens examined contained much more plant material than would be found as a rule, say, in toads (*Bufo americanus* and *woodhousii*) and red-backed salamanders (*Plethodon cinereus*).

There is internal evidence that this small sample is a representative one. The bottom row of the table lists the percentage of food items of a stomach with respect to the total of kinds of food items. Examination of these figures reveals that, out of fourteen frogs with food in their stomachs, twelve had eaten twelve or more per cent of the same kinds of foods (al- though such 'frogs came from two distant localities in the Chicago Area) and three had eaten about twenty-five per cent of the same kinds of foods.

Finally, seven food-items (beetle larvae, fly larvae, oribatid mites, collembolans, spiders, phalangids, and ants) eaten by these tree frogs are all found frequently in tree holes. Although we have not collected *versi- color* in such habitats, and have no report of such a capture in the literature, there is every reason to think that these amphibians may enter tree holes on occasion and feed on the arthropod inhabitants.

The feeding interrelations of the tree-hole niche are not too different from those of a decaying log, if the spatial limitations are kept in mind. The chief difference, in tree holes of living trees, is that the living wood is being softened by parasitic fungi rather than by saprophytic fungi, and, where the cavity opens by an orifice placed a considerable distance from the ground, certain typical floor forms would be rare to absent.

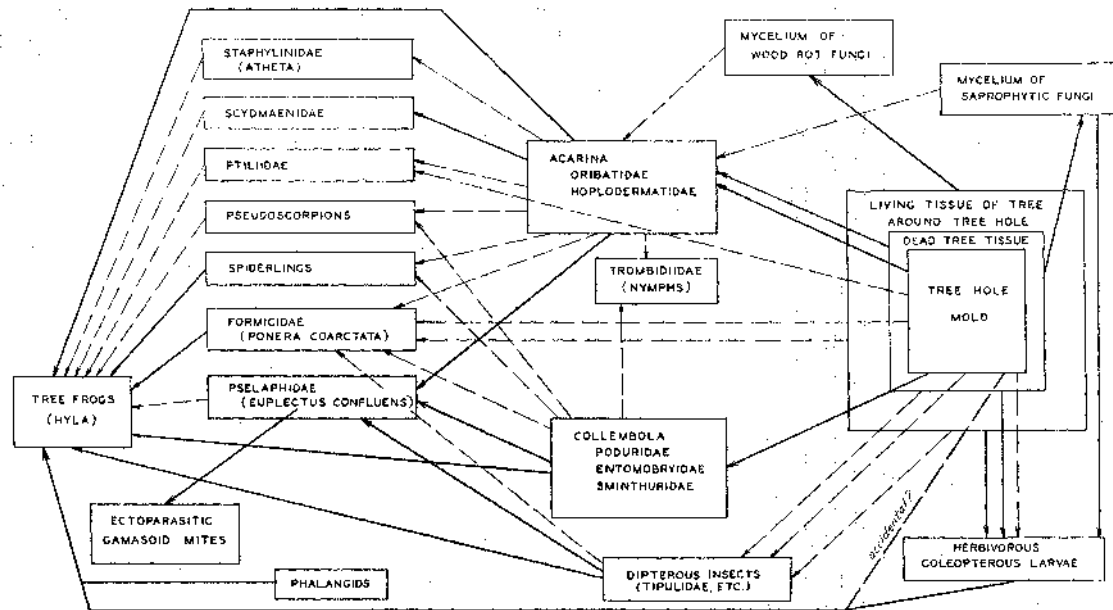
A tree-hole food web is suggested in a tentative form (Fig. 2). In this illustration the "observed" interrelations mean that a given food item has been found in the stomach of a predator, or that a given food organism has been observed being eaten by a particular predator. Obviously, the majority of the meshes of the web still lack confirmation and there are many meshes that have not been included.

Another aspect of the tree-hole community is developed in a study of the size/numbers ratio. Several tree holes were examined quantitatively. The tree-hole mold was removed and the arthropods extracted by means of a Berlese funnel, counted and measured. An example is given in Table II.

The data in Table II are presented in the form of a pyramid of numbers (Fig. 3) , in which the probable feeding categories are shown differentially. From this illustration it will be seen that the minute organisms are not only abundant but overwhelmingly herbivorous. These organisms, the

T A B L E I I
Arthropod Census of a Tree Hole

840 grams (wet weight) of a sugar maple tree hole, Number 54.			
Animal	Number in sample	Average length (mm.)	Probable feeding category
Arachnida			
Pseudoscorpionida	3	1.0-4.5	Predaceous
Araneida	3	0.3-0.8	"
Acarina			
Oribatidae	2183	0.2-1.0	Herbivorous
Hoplodermatidae	63	0.2-1.0	
Trombidiidae (nymphs)	15	0.2-1.0	Predaceous
Insecta			
Collembola			
Poduridae	243	0.2-1.0	Herbivorous
Entomobryidae	1835	0.2-1.0	"
Sminthuridae	2	0.2-0.5	"
Homoptera			
Cicadellidae	9	3.0-4.0	Herbivorous
Coleoptera larvae			
Scydmaenidae	4	1.0-2.0	Predaceous
Carabidae			
<i>Agonoderus pallipes</i>	1	5.5	
Staphylinidae			
<i>Atheta</i>	4	2.0-3.0	Predaceous
Pselaphidae			
<i>Euplectus confluent</i>	8	1.2-1.6	Predaceous
<i>Euplectus hudsonicus</i>	4	1.2-1.6	"
<i>Melba sulcatula</i>	1	1.3	
Ptiliidae	74	0.3-1.0	
Hymenoptera			
Parasitic wasps	4	0.2-1.0	Parasitic
Formicidae			
<i>Ponera coarctata</i>	1	2.5	Omnivorous
Dipterous larvae	111	2.0-3.0	? Herbivorous
Total	4600		



REPRESENTATIVE DIAGRAM OF A TREE HOLE FOOD WEB. ARROWS POINT FROM FOOD TO FEEDER. SOLID ARROWS, OBSERVED; BROKEN ARROWS, SUSPECTED.

Figure 2. Tentative food web of a tree-hole habitat. For discussion see text.

oribatid mites and collembolans, are herbivorous in the sense that they are feeding probably upon the tree-hole mold. They are not herbivorous probably in the same sense that aphids, leaf hoppers, grasshoppers, cattle and the numerous other animals are that feed on living plant tissue. Such a distinction should be drawn between these two great groups of herbivores, since the mold feeders are much nearer the functional level at which the saprophytic fungi and heterotrophic bacteria are operating.

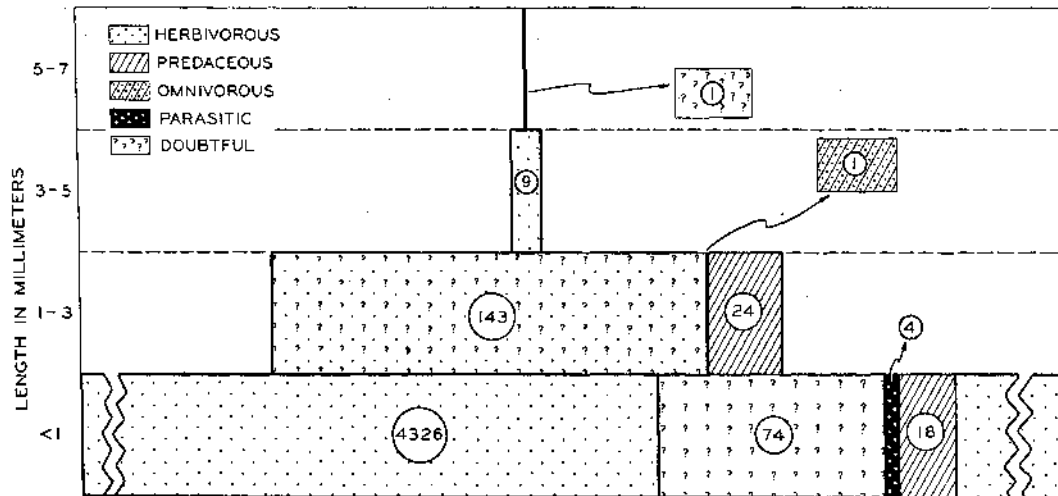
There is reason to believe that the general relationships in Figure 3 are applicable to tree-hole mold in particular and to the related log-decay cycle in a more remote way. Three such quantitative analyses were made. The three tree holes each came from a different tree, a sugar maple (Table II) , a beech, and an elm. Without repetition of detail, it may be said that all three were similar. Several suggestive comparisons of this analysis are given in Table III.

TABLE III
A Comparison of Three Tree Holes

Ratio	Elm (No. 16)	Sugar Maple (No. 54)	Beech (No. 57)
Herbivore : Carnivore	126: 1	92 : 1	8 : 1
All arthropods : grams wet tree-hole mold	4.4 : 1	5.5 : 1	5.1 : 1
Ants : other arthropods	1 : 243	1 : 4599	1 : 4.6

In Table III it will be noted that the ratio between the tree-hole population and the tree-hole mold is close—very remarkably so—between the three tree holes. All three were well developed, and the suggestion arises that between four and five arthropods per gram of tree-hole mold represents a more or less stable optimum for such habitats, under favorable conditions and in their approximate stage of development.

The greatest difference between these three habitats is in the ratio of herbivores to carnivores. For example, the elm and sugar maple have similar h/c ratios, but the beech has a very low h/c relationship. This latter is exceptional, and serves to document a point made earlier. This beech sample contained a large number of the ant, *Ponera coarctata pennsylvanica*, and it is thought that their presence in numbers (probably a nest) is responsible for the relatively small herbivore population of mites and collembolans. If this is so, then the effect of the ants may have been expressed through direct competition for the mold, or by predation on the minute arthropods. This general view coincides with field estimates that where tree holes were colonized by ants, such as *Camponotus* or *Aphaenogaster*, there was a dearth of other arthropods.



PYRAMID OF 4600 ARTHROPODS IN 840 GRAMS OF TREE HOLE MOLD IN A SUGAR MAPLE. (TREE HOLE #54.)

Figure 3. Diagram of a pyramid of numbers of a sugar maple tree hole. For discussion see text.

Two more ways in which tree holes are integrated within the larger forest community may be mentioned. First, such habitats receive many animals at the approach of winter conditions in the temperate regions, and thus serve as sites of hibernation for other than tree-hole residents. Second, it was noted that in several cases where tree holes were in trees on a flood plain of a stream that flooded this terrace in the spring, such holes were filled for some inches with silted clay. In such cases, the orifice of the tree hole was at ground level to a foot above the ground, but often the cavity extended for several feet above the high-water flood mark. Hence, it is probable that such tree holes on occasion may harbor animals that are normally residents of the floor. In both as a hibernaculum, and as a refuge in time of flood, the tree hole has a protective value for certain residents of the community in general, or for contiguous communities.

It is always difficult to judge with precision when the tree-hole complex ends and the decaying-log cycle begins. There are too many variables involved to do more than adopt a broad philosophic view of the problem. The living tree, without tree holes, may be blown down and die, in which case the normal cycle of decay sets in, until, at last, it is converted into a mounding mass of log mold by saprophytic fungi, bacteria and associated animals. This process of decay is important to the community (Fig. 1) , and the sequence of changes and the complex interactions in this microsere have been well reported (Shelf ord, 1913; Graham, 1922, 1924, 1925, 1939; Blackman and Stage, 1924; Savely, 1939 and Daggy, 1946) .

The standing, yet dying tree presents another problem in that parts of the organism are entering the decaying-log cycle at a late stage (heartwood rot) , whereas other parts are integrated with organisms that are associated only with living trees.

Few forest habitats offer a wider variety of niches, or are involved in a greater number of microseres than a tree. The organisms inhabiting the tree are generally stratified both vertically (cf. Allee, 1926) , and concentrically, and include residents and transients, subterranean and epigeal inhabitants. There are nesting birds in the branches, tree frogs and the pilot black snake may move over the trunk and branches in search of foods, aphids and coccids are sucking tree fluids. These types of arboricoles are concerned with finding shelter and/or food on or in the tree as a living organism, or as a solid substrate. Within the living tree tissues are still others, including the parasitic fungi and larvae of many wood-boring beetles, that are similarly drawing nourishment from the tree, but are wholly within the entoparasitic concept at their present life-history stages. The tree holes embrace still other biocoenoses already discussed. Here and there the saprophytic fungi are attacking the dead heartwood

and the decaying-log microsera may be operative at several points, at several different stages. Eventually the mycelium of the tree fungi develops visible fruiting bodies. These conks form the substrate for an entirely new microsera. Such mycetozoa as various fly larvae and beetle larvae attack the fungus tissues, develop there, and the adults, their predators and parasites form another biocoenose. The fungus habitat has been discussed in general terms by Allee, Emerson, Park, Park, and Schmidt (1949) ; the successional stages (Park, 1931), feeding activities (Weiss, 1920, 1920a) , analysis of activity patterns (Park, 1935, Park and Keller, 1932, Park and Sejba, 1935) have been reported. Nor must we omit mention of the ants and termites that colonize the tree, and whose complex societies contain so many interactions with the tree habitat and its occupants (Emerson, 1939, 1942).

This very inadequate summary of the tree as a habitat suggests how necessary it is to view tree holes in the broad perspective as well as from the limited viewpoint, such as is undertaken in the following section.

THE PSELAPHID BEETLE FAUNA

In the preceding section the ramifications of the tree-hole complex have been suggested, and the integration of this habitat type with the forest community has been attempted. The present purpose is to examine a limited fauna in more detail, since it allows a more precise focus on portions of species populations that are known to inhabit tree holes.

In all, 36 tree holes were examined in the manner explained earlier. The basic data of these examinations are given in Table IV.

A total of 343 pselaphids was obtained, or an average of 9 beetles per habitat. In view of the relative scarcity of pselaphids as contrasted to staphylinids, for example, this is a high average. Fifteen tree holes produced no pselaphids, so that in 21 habitats that did, the average is 16 of these beetles per habitat. Since about 58 per cent of the tree holes contained pselaphids, the conclusion is that the family is adjusted to the dark, moist, still interior of the tree hole and its associated biota.

In the first place, pselaphids are known to feed on oribatid mites, hoplodermatid mites, gamasid mites, ant eggs and larvae, collembolans, fly larvae, small flies, and pieces of earthworms (Davey, 1945; Denny, 1825; Donisthorpe, 1927; Park, 1929, 1932a, b, 1947a, b). Since fly larvae, collembolans and oribatid mites are abundant in tree-hole mold, the natural foods of the beetles are present except in abnormal situations, and are present usually in abundance.

Second, certain pselaphids have been exposed to experimental gradients in light intensity and in amount of moisture (Park, 1929, 1947b) , and were found to respond to lower light intensities and moister condi-

T A B L E I V
General Data on Tree Holes

Tree Hole (L, living tree D, dead tree))	Kind of Tree	Locality Data	Tree - Wet Hole Dry Mold wt. gm. wt. Percent of Water			Pselaphidae No. Spp. No. Indiv.	
			wt. gm.	wt.	Percent of Water	No. Spp.	No. Indiv.
1. 3 ft. from ground, L	Red Oak group	Palos Park, Cook Co., Illinois. Nov. 9, 46	—	—	--	1	2
2. Basal, L	Beech	Saugatuck, Allegan Co., Michigan. July 30, 48	—	—	----	3	49
3. 3 ft. from ground, L	Sugar Maple	Glenn, Allegan Co., Michigan. Aug. 24, 48		—			
4. Basal, D	Sugar Maple	Warrens Woods, Lakeside, Berrien Co., Mich. May 7, 49	360	—	—	0	0
5. Basal, L	Beech	Warrens Woods. May 7, 49	2912	1008	65	6	23
6. 6 in. from ground, D	Silver Maple	Tuscola, Douglas Co., Illinois. June 13, 49	—	—			
7. (no. 6 for 2nd sample)	Silver Maple	Tuscola June 29, 49	10360	—		2	2
8. Basal, L	Hemlock	Glenn, July 3, 49		3150	--	1	8
9. Basal, L	Sugar Maple	Glenn, July 3, 49	1148	504	56	1	8
10. (no. 2 for 2nd sample)	Sugar Maple	Glenn, July 3, 49 (full of water)		?	90 ?	0	0
11 Basal, L	Sugar Maple	Douglas, Allegan Co., Michigan. July 4, 49	—	1120		2	18
2. 61/2 ft. from ground, L	Beech	Saugatuck. July 4, 49	112	28	75	0	0
13. Basal, L	Beech	Saugatuck. July 4, 49	840	224	73	1	32
14. Basal, L	Beech	Douglas. July 4, 49	4844	—	—	2	66
15. 12 in. from ground, L	American Elm	Carle Woods, Des Plaines, Cook Co., Ill. July 16, 49	1344	782	41	0	0
16. 12 in. from ground, L	American Elm	New Lennox, Will Co., Ill. July 16, 49	532	518	2.6	1	1
17. Basal, L	Jack Pine	Ogden Dunes, Porter Co., Ind. July 20, 49	518	448	14	0	0
18. Basal, L	Red Oak	Palos Park. July 22, 49	420	224	47	0	0
51. Basal,	Beech	Warrens Woods. July 30, 49	2884	700	76	0	0
52. 16 in. from ground, L	American Elm	Warrens Woods. July 30, 49	7616	1512	80	1	16
53. Basal, L	Sycamore	Warrens Woods. July 30, 49	316	112	64	0	0
54. Basal, L	Sugar Maple	Warrens Woods. July 30, 49	840	252	70	3	13
55. Basal, L	Beech	Warrens Woods. July 30, 49	1876	896	52	1	1
56. Basal, D	Beech	Warrens Woods. July 30, 49	2940	560	81	3	29
57. 8 in. from ground, L	Beech	Warrens Woods. July 30, 49	4284	1512	65	4	29
58. Basal, L	Beech	Warrens Woods. July 30, 49	2828	812	71	1	8
59. 7 in. from ground, L	Sugar Maple	Warrens Woods. July 30, 49	476	140	7 0	0	0
60. 11 in. from ground, L	Box Elder	Evanston. Aug. 8, 49 (<i>Camponotus nest</i>)	112	28	75	0	0
61. 12 in. from ground, L	Hard Maple	Palos Park. Aug. 13, 49	560	196	65	0	0
62. Basal, L	Black Oak group	Palos Park. Aug. 13, 49	1456	1008	31	0	0
63. Basal, L	Swamp White Oak	Palos Park. Aug. 13, 49	1092	196	82	0	0
64. Basal, L	Black Oak group	Palos Park. Aug. 13, 49	2030	448	78	2	3
65. Basal, L	Swamp White Oak	Palos Park. Aug. 13, 49	1932	952	5	1	1
66. Basal. L	Ash sp.	Glenn. Aug. 16, 49 —	1680	1260	25	0	—0
67. Basal, L	Beech	Glenn. Aug. 16, 49	2240	868	61	1	31
68. Basal, D	Pine sp.	Amberg, Marinette Co., Wisconsin. Aug. 21, 49	2716	1274	53	1	

tions. Such responses would tend to retain these beetles in such dark, moist habitats as leaf mold, log mold, and tree-hole mold.

Moisture is important in the differential distribution of pselaphids in tree holes, either directly, or indirectly through a regulation of their food supply. In the present study, 61,268 grams of wet mold were taken from 29 tree holes. The maximum sample was 10,360 grams and the minimum sample was 112 grams, and the average was 2112 grams. In these 29 habitats with wet mold there were 264 pselaphids, or 9 pselaphids per tree hole having wet mold. In other words, the survey found one pselaphid per 232 grams of wet tree-hole mold.

Of the total of 343 pselaphids collected, 264 (76 per cent) were taken in wet mold. This is a high proportion, but does not tell us how "wet" the mold should be. No direct evidence is at hand, as this must be obtained by controlled experimentation, but the field work on this point is significant. It will be seen from Table IV that the water content of the wet mold was obtained in 27 out of 36 samples. Analysis of these data shows that the greatest yield of pselaphids was from mold with a free water content of between 61 per cent and 81 per cent. No pselaphids were obtained from samples with a water content below 50 per cent or above 85 per cent. Consequently, the field data substantiate experimental work previously reported.

Third, where ants were nesting in the tree hole, the non-myrmecophilous pselaphid fauna was reduced in numbers or absent; this was checked in the case of *Ponera coarctata* (Table III), and for *Aphaenogaster* and *Camponotus*. This general situation has been discussed previously (p. 32).

Fourth, there was a decrease in the average number of pselaphids with increase in height of the tree-hole orifice above the ground level. Thus, for basal tree holes the average was 14 beetles; at six to eight inches, 8; at twelve to sixteen inches, 4; at four feet, none; at seven feet, none. The small number of samples precludes the wording of a definite conclusion, since pselaphids can climb, and probably will be found to occur in high tree holes, but the general tendency seems clearly established.

Fifth, there was a differential distribution of pselaphids in tree holes of various kinds of trees. Where more than one sample was collected from the same species of tree, so that averages could be obtained, it was found that beech had a large population of 24 pselaphids per tree-hole mold-sample, sugar maple and elm were tied with an average of 6, red oak with 1, and swamp white oak with 0.5.

This trend suggests that, other things being favorable, pselaphids are more abundant in the tree holes of dominant tree species (beech, sugar maple, elm) . This is compatible with previous findings, that these beetles are characteristically abundant in climax forests, whether in the

tropics, subtropics, or temperate regions. Such forests have a relatively rich floor mold, and a well developed stratification of vegetation; also low interior light intensity, low evaporation rate, and a high relative humidity and soil moisture. Such trees are frequently parasitized by numerous woodrot fungi and basal tree holes are common, as noted previously.

The beech trees, in particular, had a high yield of tree-hole pselaphids; e.g., 268 beetles from eleven samples. In ten of these samples, wet weight of the mold was obtained, and 219 pselaphids were taken from these ten, or an average of 22 pselaphids per beech tree hole where wet weights of mold were known. This works out at one pselaphid per 109 grams of wet beech mold, whereas there was only one pselaphid to 232 grams of wet tree mold of all tree species.

Sixth, the pselaphid fauna of tree holes in the area covered is abundant, relatively, in terms of number of species. These data are given in Table V.

From this table it will be seen that twelve species were collected, divided among seven genera. Three tribes are represented. The Batrisini, with two species of *Batrisodes* reported, are well known as inhabitants of ant nests and log mold (Park, 1947b) ; the Trichonychini is represented by a species of *Rhexidius*, known to occupy a variety of forest floor niches; the overwhelming majority of species in tree holes, nine species in five genera, belong to the Euplectini. This tribe is characteristic also of forest leaf mold, forest log mold, and prairie sod mold (Park, Auerbach, and Wilson, 1949).

One species, *Euplectus confluens*, appears to be the dominant population in tree-hole mold of the region, certainly it is the most abundant in the present survey. For example, of 343 pselaphids collected, 275 were of this species. In other words, *Euplectus confluens* accounted for 80 per cent of the total. In eight tree holes this species was the only pselaphid present, out of 21 that yielded these beetles.

Euplectus is a large genus, and contributed the most species to the census (Table V) . *Euplectus confluens* is one of the most common species of the genus in eastern North America, and is prevalent in log mold, so that its abundance in tree holes is to be anticipated, but hardly its preponderant position. This euplectine would appear to be quantitatively more abundant per volume of tree-hole mold than for the same volume of log mold. In other words, the species is adjusted particularly well for the tree-hole habitat.

Euplectus confluens was found in tree holes of a variety of trees: 8 beech, 223 beetles; 3 sugar maple, 27 beetles; 1 elm, 16 beetles; 1 hemlock, 8 beetles; 1 swamp white oak, 1 beetle.

This species is so preponderant that its population tends to skew general conclusions concerning tree-hole pselaphids. This should be

TABLE V

Pselaphid Beetles Collected

No.	Species	Males	Females	Total (p)	No. times species collected (f)	Rank by no. individuals	Tree Hole Index f
1	<i>Thesium carifrons</i> , Pl. III	2	1	3	2	6th	0.16
2	<i>Euplectus confluens</i> , Pl. IV	76	199	275	14	1st	106.00
3	<i>Euplectus hudsonicus</i>	4	0	4	1	5th	0.11
4	<i>Euplectus linearis</i>	1	0	1	1	7th	0.02
5	<i>Biblopectus integer</i>	4	6	10	3	4th	0.83
6	<i>Melba sulcatula</i> , Pl. V	6	4	10	4	4th	1.11
7	<i>Melba maja</i>	0	1	1	1	7th	0.02
8	<i>Trimiopectus obsoletus</i>	10	10	20	4	2nd	2.22
9	<i>Trimiopectus auerbachii</i>	3	0	3	3	6th	0.25
10	<i>Rhescidius canaliculatus</i> , Pl. VI	4	7	11	4	3rd	1.22
11	<i>Batrissodes globosus</i>	1	3	4	2	5th	1.66
12	<i>Batrissodes furcatus</i>	0	1	1	1	7th	0.02
Totals		111	232	343			

n = total number of tree holes berlesed; e.g., 36.

kept in mind, since it is possible that another survey in another part of the North American deciduous forest biome might show a different picture of tree-hole pselaphids.

For example, we have noted that (1) best yields were in tree-hole mold having from 61 to 81 per cent free water content; (2) that there was an average of 22 pselaphids per beech tree hole, where wet mold weights were taken; (3) that there was one pselaphid per 109 grams of wet beech mold.

If these three statements are applied to *Euplectus confluens* we find that (1) best yields were in tree-hole mold having from 61 to 81 per cent free water content (average 69 per cent); (2) that there was an average of 19 individuals per beech tree hole, where wet mold weights were taken; (3) that there was one individual per 127 grams of wet beech mold.

It is well known that gamasoid mites are associated often with beetles, either as phoretics or ectoparasites. On one occasion, a sample from a basal beech hole (July 4, 1949 at Saugatuck, Michigan) yielded 3 males and 29 females of *Euplectus confluens*. Of these, 12 females were parasitized by gamasoids, each female having from 2 to 12 mites.

Finally, an effort was made to rank the several pselaphid populations collected by a Tree Hole Index $\frac{fP}{n}$, where f is the number of times

a species was collected, p is the total specimens collected for a species, and n is the total number of tree-hole samples examined. These data are given in the last column of Table V, and it will be noted that *Euplectus confluentis* has a distinctive tree-hole index value.

In conclusion, for those interested biologists who are unfamiliar with these minute beetles, four species have been illustrated (Pl. III, IV, V, VI) with meticulous attention to structural detail.*

For practical purposes, those wishing to obtain Pselaphidae in sufficient numbers for research may have a better than average chance if they will collect moist mold from basal tree holes in beech trees, and then extract the living pselaphids by a Berlese funnel into Petri dishes that have been prepared with wet filter paper.

SUMMARY

A tree hole is defined as any extrinsically produced tree cavity that is in direct contact with the external environment at some point in its development. There are subterranean tree holes (root holes) and epigeal tree holes (tree holes in the usual sense). Tree holes vary in size, shape, height above ground, and in microclimate and biota. Usually, such habitats are initiated by a bark fracture and their progress is controlled by weathering and attack by parasitic fungi primarily.

Environmental agencies instrumental in tree-hole formation are divisible into (1) physical factors, including fire, storm winds, ice splits, lightning splits, and such weathering influences as rain, snow, ice, and wind erosion; (2) biotic factors, including age and condition of tree, bacteria, parasitic fungi, saprophytic fungi, and a variety of animals. Fire, and the mycological aspects are emphasized.

* These plates have been drawn by Miss Marie Wilson, an experienced illustrator of this family of beetles, and under the constant supervision of the senior author. The routine was as follows. A typical specimen was selected, and its structural features observed at 70 diameters. In this preliminary conference the range in variation of structure in the population was noted and "key characters" checked. Then the artist drew the beetle by means of a reticule in one of the oculars of a dissecting binocular, transferring the detail seen under each reticule square to a square of a sheet of graph paper. The completed drawing was then gone over by the senior author and checked or altered by the artist. The approved drawing was then transferred to drawing paper by means of an illuminated glass-topped drawing table. This drawing was then inked, and the finished plate checked again by the senior author. Each plate required about twenty hours.

Under exceptional circumstances the tree-hole orifice may heal over. Usually, the development is either through an aquatic microsere, or a terrestrial microsere, depending upon position of orifice, climate, latitude and edaphic factors. In the aquatic microsere, the biotic agents include plankton, tree-hole mosquito larvae, both plankton feeders and predators, and amphibians.

If the terrestrial microsere is involved, biotic agents include owls, woodpeckers, deer mice, flying squirrels, their diverse ectoparasites, comb-making bees, ants, numerous beetles, crane flies, adult mosquitoes, collembolans, spiders, phalangids, pseudoscorpions and diverse mites.

No tree frogs were found in tree holes, but they may occur there on occasion. A series of *Hyla versicolor* stomachs contained, in order of abundance, ants, plant materials, phalangids, heteropterans, oribatid mites and various insects and arachnids. Seven food items (beetle larvae, fly larvae, oribatid mites, collembolans, spiders, phalangids, and ants) eaten by these frogs are all commonly found in tree-hole mold.

The tree-hole complex is discussed with reference to food-web, pyramid of numbers, and its integration with the conk microsere, and decaying-log microsere. Several tree holes were analyzed quantitatively with reference to the arthropod fauna.

The pselaphid beetle fauna of tree holes is given especial attention. Thirty-six tree holes were studied. From these, 343 pselaphids were obtained from twenty-one tree holes. Moisture is important to this beetle fauna. The survey found one pselaphid per 232 grams of wet mold, and 76 per cent were collected in wet tree hole mold. The greatest yield was in mold with a water content between 61 and 81 per cent. The pselaphid population was found to be very low in tree holes that were occupied by nesting ants. The average number of pselaphids decreased with increase in height of tree hole above the ground level. Other things being equal, the order of pselaphid abundance for kinds of trees was beech, sugar maple, elm, red oak, and swamp white oak. Basal beech holes were especially productive. There was one pselaphid per 109 grams of wet beech mold.

Seven genera, and twelve species of Pselaphidae were obtained, of which one species, *Euplectus confluent*, was especially abundant, composing 80 per cent of all pselaphids collected. These twelve species are ranked by means of a tree-hole index formula.

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PLATE I**Variation in Tree Holes**

1. Basal tree hole, in hemlock. This cavity housed a nest of a small mammal.
2. Basal tree hole with irregular orifice, in an ash.
3. Tree hole in beech, with fusiform orifice three inches above ground.
4. Basal tree hole in beech, with long cleft orifice.

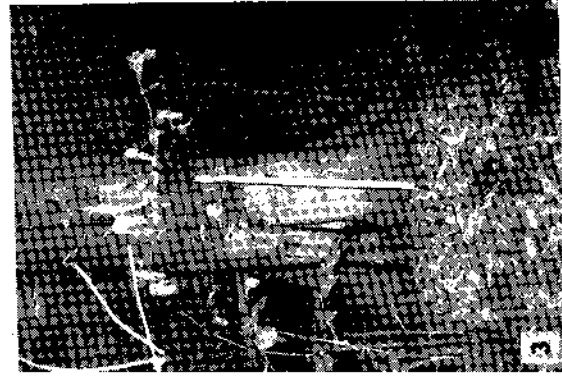
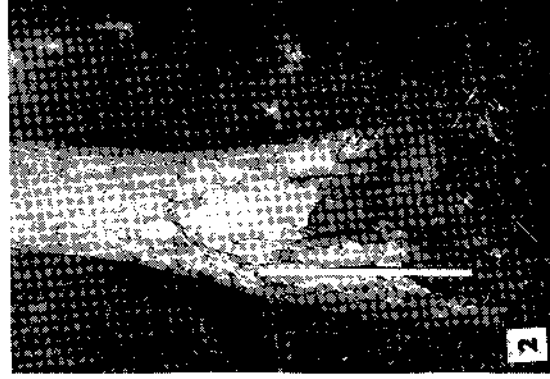
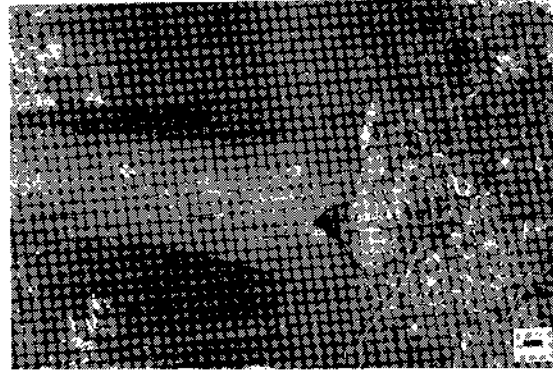


PLATE II**Variation in Tree Holes**

1. Oval orifice of tree hole in oak, four feet above ground.
2. Basal tree hole in oak.
3. Oak with three orifices, thirty-three feet above ground.
4. Oak with three factors in the tree-hole complex indicated by horizontal lines: upper, fungus conk; middle, incipient tree hole; lower, bark off, to show orifices of burrows of wood-boring beetle larvae.

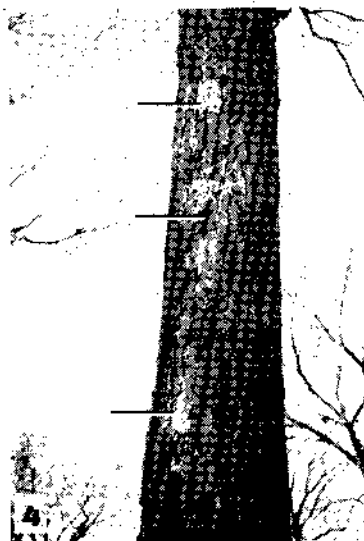
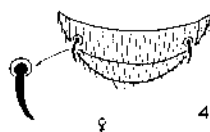
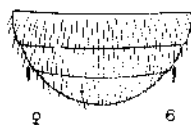
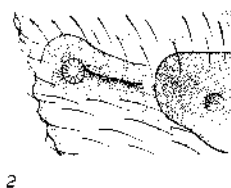
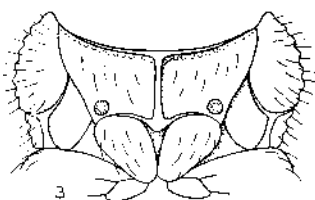
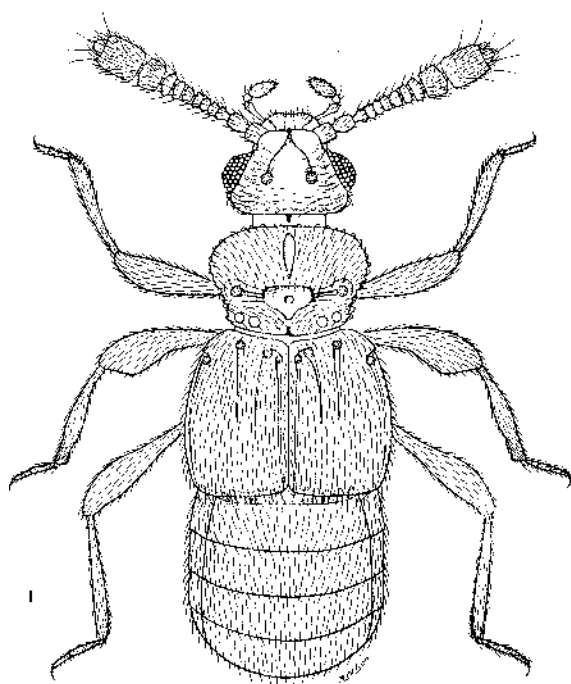


PLATE III

Thesium cavifrons (LeConte)

1. Dorsal aspect of male, 70x.
2. Detail of left side of transverse pronotal sulcus, 70x.
3. Prosternum, to show bisecting longitudinal carina, 70x.
4. Apical tergites of female, to show spinoid pencil of what appears to be agglutinated setae, each side, 70x.
5. Terminal venter of male, to show simple seventh visible sternite, 70x.
6. Terminal venter of female, to show fourth to sixth (terminal) sternites, 70x.



P L A T E I V

Euplectus confluens LeConte

1. Dorsal aspect of male, 70x.
2. Maxillary palpal cone, surface layer, 920x. Note what appear to be minute apical pores, connected with fine canals.
3. Maxillary palpal cone, 920x, median layer. Note central core, and contrast with alpha antennal cones for similar structure.
4. Tenth and eleventh antennal segments, 920x. Note simple setae; long, slender alpha cones, with central core; two groups of short, thick beta cones of apparently homogeneous structure.
5. Stereogram of eleventh antennal segment, to show ring of eight alpha cones, and eight beta cones in two groups of four each, each group in a lateral concavity at apical fourth.
6. Fourth to seventh sternites of male, 70x.
7. Fourth to sixth sternites of female, 70x.

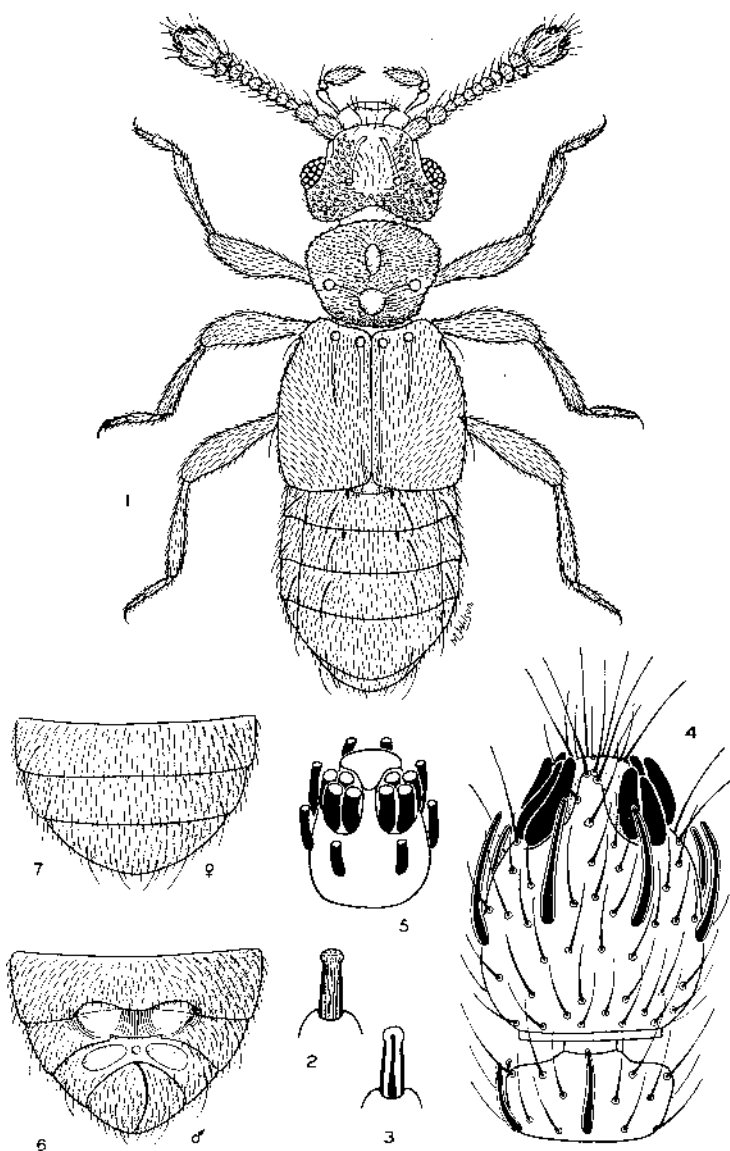


PLATE V*Melba sulcatula* (Casey)

1. Dorsal aspect of male, 70x.
2. Maxillary palpal cone, note central core, 920x.
3. Tenth and eleventh antennal segments, to show alpha antennal cones, 920x.
4. Capitae setae from ventral surface of head, 70x.
5. Mesotrochanter of male, 70x.
6. Apex of mesotibia of male, to show two padules, 920x.
7. Lateral face of left elytron, to show oblique pleural carina, 70x.
8. Fourth to seventh sternites of male, 70x.
9. Fourth to sixth sternites of female, 70x.

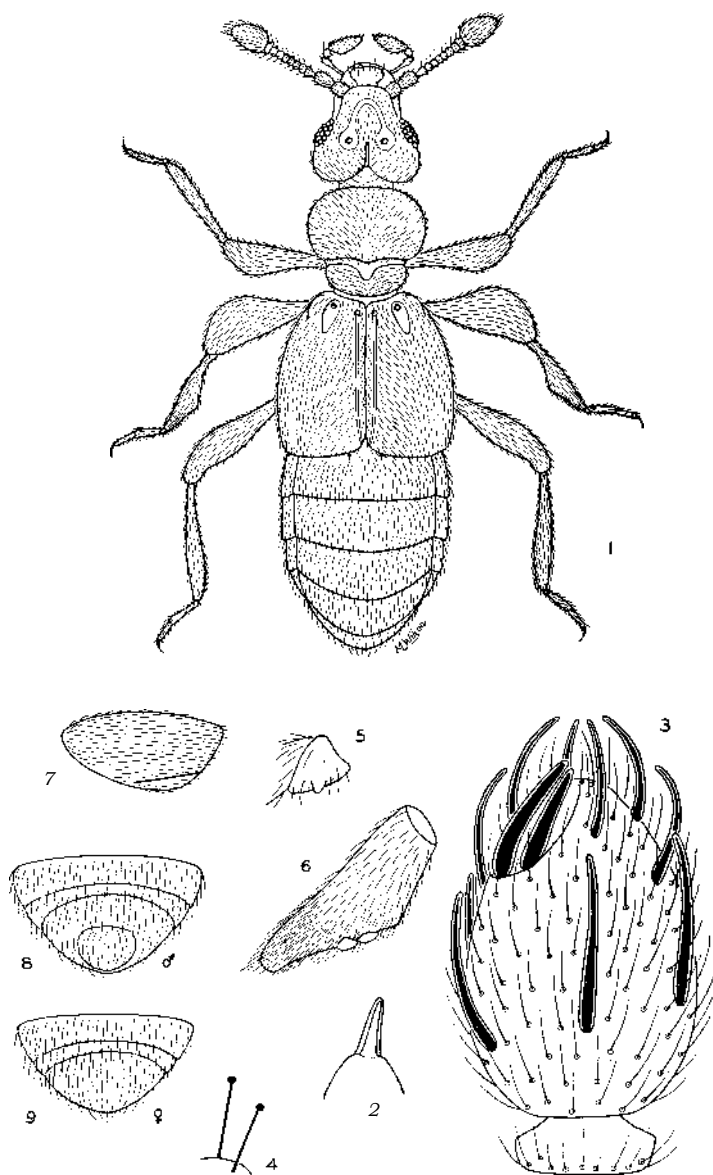


PLATE VI

Rhexidius canaliculatus (LeConte)

- 1. Dorsal aspect of male, 70x.**
- 2. Lateral aspect of head to show genal beard, 70x.**
- 3. Minutely capitulate seta and normally aciculate setae of genal beard, 920x.**
- 4. Maxillary palpal cone, 920x.**
- 5. Tenth and eleventh antennal segments, to show alpha antennal cones, 920x.**
- 6. Detail of an antenna! cone, 920x.**
- 7. Transverse frontal sulcus of male, to show median horn, 70x.**
- 8. Simple transverse frontal sulcus of female, 70x.**
- 9. Lateral face of left elytron, to show subhumeral fovea and longitudinal carina, 70x.**

